session 1 (compared to David's 27 during session 1), and Dennis' mother did not start production at all until session 2. In addition, the children produced many more multisign phrases conveying semantic relations than did their mothers. Over the course of the four interviews, David and Dennis produced 127 and 42 such phrases, respectively, while their mothers produced only 41 and 13, respectively. There is thus no evidence that the children learned to concatenate signs to express semantic relations by imitating their mothers' gestures.

Finally, the children were far more likely than were their mothers to use characterizing signs in their multisign phrases. The mothers produced as many characterizing signs in single-unit phrases as their children but far fewer characterizing signs in multisign phrases (Table 1, columns 2 and 3). Consequently, there is no indication that the children learned to integrate their characterizing signs into an ordered system by imitating their mothers' productions (*11*).

We have shown that a child can develop a structured communication system in a manual mode without the benefit of an explicit, conventional language model. This achievement is cast into bold relief by comparison with the meager linguistic achievements of chimpanzees. While chimpanzees seem to learn from manual language training (*12*), they have never been shown to spontaneously develop a language-like communication system without such training—even when that chimp is lovingly raised at a human mother's knee (*13*). On the other hand, even under difficult circumstances, the human child reveals a natural inclination to develop a structured communication system.

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References and Notes

1. Deaf children who are orally trained are instructed in lipreading and in speech production with no audio feedback. These children have been observed to spontaneously gesture to one another "behind the teacher's back." [L. Fant, *Ameslan* (National Association of the Deaf, Silver Spring, Md., 1972); B. T. Tervoort, *Am. Ann. Deaf* **106**, 436 (1961)].
2. A rationale and justification of our coding methods and a more detailed discussion of results are given by H. Feldman, S. Goldin-Meadow, and L. Gleitman [*Action, Gesture, and Symbol*, A. Lock, Ed. (Academic Press, New York; in press)].
3. Communicative signs were motor behaviors, directed to a person, which served no direct function in the setting. The physical form of the signs was described by a system similar to the one used to describe American Sign Lanuage. The dimensions used in the descriptions are described by W. C. Stokoe, Jr. [*Stud. Linguist. Occas. Pap. 8* (1960)].
4. A detailed account of the criteria for single signs and an account of the lexical data are given by H. Feldman [thesis, University of Pennsylvania (1975)]; the criteria for sign phrases and for the data on syntactic and semantic relations are described by S. Goldin-Meadow (*Stud. Neurolinguist*, in press).
5. A description of the method of rich interpretation is given by L. Bloom [*Language Development* (MIT Press, Cambridge, Mass., 1970); *One Word at a Time* (Mouton, The Hague,1973)].
6. The system we use to describe the deaf child's phrases is an adaptation of the case system presented by C. J. Fillmore [in *Universals in Linguistic Theory*, E. Bach and R. T. Harms, Eds. (Holt, Rinehart & Winston, New York, 1968), pp. 1–88].
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8. The children produced a third type of sign, the marker, which did not refer to things and events but rather served modulation functions. Sign markers were head nods and side-to-side head shakes and were reminiscent of words such as "yes" and "no" in English; for instance, in the sentence "There are no trucks," the "no" modulates, in particular negates, the existence of trucks.
9. The data in Fig. 1 include only two-sign phrases. We exclude phrases containing three elements (such as point at book, "give" sign, point at self, to request that the book be given to the child) and also exclude phrases containing either repeated elements or simultaneously sign elements (such as point at book, "give," point at book; or point at book signed simultaneously with "give"). In addition, we exclude all phrases containing points at pictures because the children tended to point at pictures before producing other signs. The pictures pointed at were often facsimiles of objects playing the patient role; thus, we would have, perhaps artifactually, inflated our patient-first orderings if we had included these phrases. As a result, Tracy (observed for two sessions at 4 years 1 month and 4 years 3 months) was not included in this analysis because she produced very few action phrases which did not contain points at pictures. The data that appear in Fig. 1 represent 64, 83, 92, 70, and 86 percent of all the two-sign, pictureless action phrases produced by David, Dennis, Donald, Kathy, and Chris, respectively.
10. The following conventions are used in describing the order rule: (i)→ indicates that the symbol on the left can be rewritten as the symbol or symbols on the right. The order of the symbols on the right must be maintained in the rewriting process. (ii) ( ) indicates that the symbol in the parentheses is optional, that is, it either can or cannot be chosen in the rewriting process.
11. S. Goldin-Meadow and H. Feldman [*Sign Lang. Stud.* **8**, 225 (1975)].
12. R. A. Gardner and B. T. Gardner, *Science* **165**, 664 (1969); B. T. Gardner and R. A. Gardner, *Behav. Non-Hum. Primates* **4**, 117 (1971); A. J. Premack and D. Premack, *Sci. Am.* **227**, 92 (October 1972). Gardner and Gardner report that Washoe has invented signs for certain objects; although striking, this accomplishment does not address the issue of whether or not Washoe would invent such signs if she had not been exposed to a standard manual language model.
13. C. Hayes, *The Ape in Our House* (Harper, New York, 1951); W. N. Kellogg, *Science* **162**, 423 (1968). Although the Kellogg chimpanzee Gua occasionally did gesture (such as protruding lips toward a cup to mean "drink"), her gestures appeared to be far less explicit than our deaf children's signs (such as tilting a C-shaped palm toward the mouth several times without the cup in the hand, which was David's signs for "drink"); moreover, Gua did not combine signs into phrases as did our deaf children.
14. We thank D. Burke, J. Huttenlocher, K. Kaye, J. McClelland, and B. Meadow for reading earlier versions of this paper; E. Newport for helpful suggestions; L. Tefo and B. Gray for help in coding videotapes; our subjects and their families for continued cooperation throughout the study; and L. Gleitman for contributions to both our thoughts and language. Supported by a Spencer Foundation grant to S.G.-M. and H.F. while they were students at the University of Pennsylvania, an NSF graduate fellowship to H.F., an American Association of University Women predoctoral fellowship to S.G.-M., NIH training grant HD 00337 under the direction of J. Aronfreed, and NIH research grant HD 52744 to R. Gelman.

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Relative Fecundity and Parental Effort in Communally Nesting Anis, *Crotophaga sulcirostris*

Abstract. *The contribution of eggs to the communal clutch by females of the group and the genetic contribution by males of the group are significantly skewed. The amount of parental care performed by each bird is correlated with relative egg ownership for both sexes.*

True communal nesting, in which several females regularly deposit their eggs into a single nest, is now known to occur in a number of avian species such as rheas, tinamous, anis, ostriches, magpie geese, and pukekos (*1*). While the cooperative nature of this breeding system has been emphasized, the degree of skew in the clutch sizes of communal females has not been reported for any of these species. If the number of eggs the group can incubate or raise successfully is limited, females should attempt to ensure that the largest possible fraction of the communal clutch is theirs.

A phenomenon commonly observed in some of these species is the presence of eggs strewn about in the vicinity of the nest. Several explanations of this apparent wastage have been offered, usually in terms of negligence, poor breeding synchrony, improperly built or unfinished nests, the onset of male incubation, or predators (*1*). As part of a broader study of communal nesting in groove-billed anis (*Crotophaga sulcirostris*), I examined this question of egg loss and its implications. I report here that (i) egg losses are a direct result of competition among females, (ii) egg losses create a skew in the egg contribution of each female to the communal clutch, and (iii) the amount of parental care is correlated with relative egg contribution for both males and females (*2*).

Nesting groups of groove-billed anis consist of from one to four monogamous pairs. Such breeding units are stable throughout the long breeding season, during which several nesting attempts may be made. In most cases, all adult females in the group lay eggs in each successive nesting attempt (*3*). Both males and females help to incubate the eggs and feed the altricial nestlings. The nest is a bulky open cup made of twigs, which may be situated low in marshy vegetation or high in a tree.

One or more eggs can usually be found on the ground under nests with two or more laying females; in contrast, eggs are never found under nests with a single breeding female. In communal nests in which new eggs were marked each day, all eggs were initially laid in completed nests. All of the early-laid eggs were discovered on the ground under the nest 1 or 2 days after laying. At some point the losses abruptly stopped and the clutch accumulated to completion.

Observations at nests during the early laying period revealed that the females in a communal group were deliberately rolling each other's eggs out of the nest. Fifty-four nests were monitored during laying to make an exact account of the total eggs laid, tossed, and incubated. As the number of laying females increases, the average number of eggs laid per female increases (3.9, 4.8, 5.3, and 5.8 eggs per female for groups with one, two, three, and five females, respectively) and the proportion of eggs tossed also increases (0, 20, 27, and 31 percent, respectively). The number of incubated eggs per female was therefore the same for all group sizes (3.9, 3.9, 3.9, 3.8, and 4.0 incubated eggs per female for groups of one, two, three, four, and five females, respectively) (*4*).

The uniformity of the adult-to-incubated egg ratio for all group sizes, despite the larger number of eggs laid per female in larger groups, suggests a limitation on the number of nestlings a group can feed and defend. "Nestling slots" are thus limited, and competition among breeding pairs for these slots can be expected. In order to determine which birds were tossing out which eggs and whether egg tossing was equal for all females, a continual watch was made throughout the entire laying period (20 days) at a nest (Stonegate) with three laying females. A female tossed eggs out only before she laid her first egg. This pattern suggests that females do not recognize their own eggs in a mixed clutch but perceive as foreign only eggs laid before their first. As a result, early-laying females lose more eggs than females laying later, and the last-laying female loses no eggs.

Having determined the typical sequence of laying, tossing, and timing, as well as the extent of variation in egg shape and coloration for a female, I could infer egg ownership in nests monitored daily and assign each egg to the first, second, or third female in different group sizes (Table 1). Not only do earlier-laying females own a consistently smaller proportion of the incubated eggs, but the last-laying female owns an increasing number of eggs per nest as the number of females increases.

Although the last-laying female gains an apparent advantage over the early-laying females, the latter appear to have evolved strategies that minimize the amount of skew in egg contribution. One tactic is the laying of a larger total clutch. Early-laying females laid significantly more eggs than the last-laying female (two-pair and three-pair groups pooled, Mann-Whitney $U = 155$, $n_1 = 13$, $n_2 = 17, P < .05$) (Table 1). The typical difference in total clutch sizes is one to two eggs. Early females frequently lay one egg late in the cycle, well after their other eggs and often coinciding with the last egg of the last-laying female. A second tactic is to increase the inter-egg interval during the tossing phase of laying, which reduces the number of eggs tossed. Inter-egg intervals for early-laying females were 3 days for the first few eggs and 2 days for most of the clutch; the last-laying female laid all eggs at 1- and 2-day intervals. A third skew-reducing mechanism involves the timing of the onset of laying and the initiation of incubation. The time interval between the first eggs of the first and last females varies from 2 to 8 days in two-female groups and from 7 to 12 days in three-female groups. The longer the last-laying female delays her clutch, the more eggs she will toss and the greater the skew will be in her favor. However, an upper limit is imposed by the commencement of incubation by the early females as they finish laying. Eggs laid late hatch late, and younger nestlings naturally are

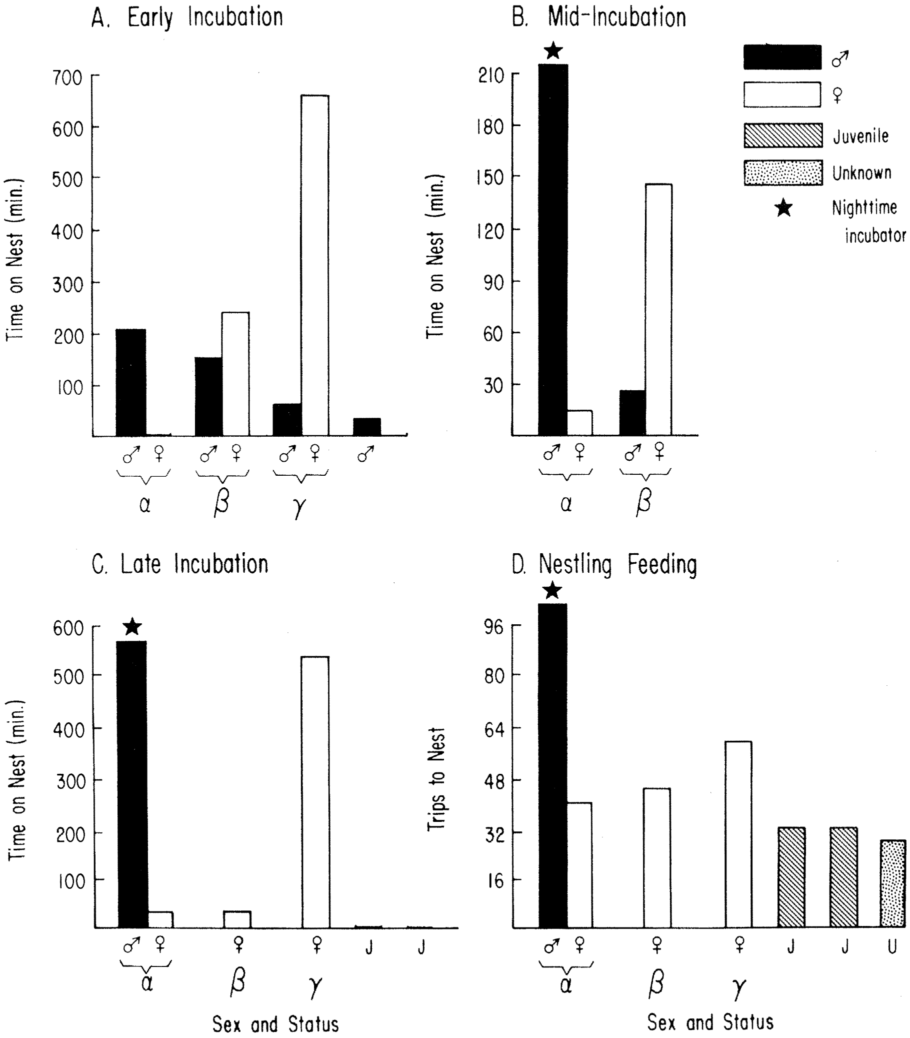

Fig. 1. Contributions of individual alpha, beta, and gamma birds to incubation and feeding of nestlings. (A) Three-day total of incubation effort for Pink group during early incubation period (alpha female had not finished laying). (B) One-day total of incubation for Glanders group during middle of incubation. (C) Two-day total of incubation for Stonegate group during the last days of incubation. (D) Three-and-one-half-day total of nestling feeding trips for Stonegate group.

Table 1. Average skew of egg ownership for one-, two-, and three-female groups.

Order of laying	Laid (No.)	Tossed (No.)	Incubated	
			No.	Proportion
One-female groups (N = *19)*				
	3.9	0.0	3.9	1.00
Two-female groups (N = *9)*				
First	5.1	2.6	2.5	.37
Second	4.3	0.0	4.3*	.63
Three-female groups (N = *4)*				
First	7.0	4.0	3.0	.24
Second	6.3	2.5	3.8	.30
Third	5.8	0.0	5.8†	.46

*Number of incubated eggs for first versus second females, Mann-Whitney $U = 72.5$, $P < .005$. †Number of incubated eggs for first and second females (pooled) versus third female, $U = 30$, $P < .01$.

smaller than their older nestmates [Spearman rank correlations at one nest ($N = 12$) of laying date versus hatching date, $r_s = .875$, $P < .01$; hatching date versus wing length, $r_s = .956$, $P < .01$; laying date versus wing length, $r_s = .811$, $P < .01$]. Smaller nestlings had lower chances of survival than larger nestmates [regression of percent survival on percent of smaller nestmates, $r = .81$, $P < .01$, $N = 10$ (*5*)], with survival rates of about 60 percent for the largest nestling and 23 percent for the smallest. Consequently, a last-laying female that delays too long will increase the proportion of her eggs in the nest but will reduce the survival rate of her nestlings. Last-laying females apparently do not delay to the point at which their nestling survival is lowered, since they did not own a significantly greater proportion of the late eggs (fraction of incubated eggs laid earlier for last-laying female versus all other females, two- and three-female groups pooled, $t = 1.55$, $N = 84$, $.1 < P < .2$).

The key factor maintaining the egg ownership skew appears to be the ability of the last female to lay eggs more rapidly. Last females laid eggs at significantly shorter intervals than earlier females ($U = 649.5$, $n_1 = 21$, $n_2 = 48$, $P < .05$). As an example, inter-egg intervals in the Stonegate group averaged 2.6 days for the first female, 1.8 days for the second, and 1.5 for the third female. Since the effect of laying larger total clutches by early females is to compensate for tossed eggs, an inverse relationship appears to exist between rate of laying and total clutch size. The critical effect of egg tossing may therefore be to exhaust the energy reserves of early females, which reduces their rate of egg production during the laying period of the last female. Thus for energetic reasons alone, early females cannot eliminate the skew created by egg tossing.

The egg-laying strategies of the females in a group have evidently evolved as a series of competitive adaptations and counteradaptations, arising from selection on females to get the largest proportion of their eggs into the nest. The number of eggs a female contributes to the communal clutch ultimately depends on the order of the onset of laying. The sequence of laying was the same in subsequent nesting attempts of three groups for which this information was available. The females in a group can therefore be ranked in order of decreasing number of incubated eggs with the alpha female laying last and incubating the most eggs. Females of high status were consistently older than lower-status females [sign test, $x(-) = 0$, $N = 6$, $P = .03$]. Males can be similarly ranked by assigning them the same status as the female to which they are mated. Although exact paternity was not determined, adulterous matings are rare compared to within-pair matings [see also (*6*)], and males vigorously defend their mates against other males in the group. Male status correlated well with size [sign test, $x(-) = 3$, $N = 32$, $P < .001$] but not with age. This rank order, based on laying sequence, reflects not only relative clutch size but also, presumably, the relative production of juveniles by pairs of different status. All females suffer equally from the effect of egg age on nestling survival. Furthermore, adults recognize neither their own eggs nor their nestlings, so no opportunity for preferential feeding of one's own offspring is available. The probability of nestling loss is therefore equal for each pair, and the skew in young fledged is likely to be the same as the skew in clutch sizes.

Differences in clutch size are correlated with the amount of parental care contributed by group members. Incubation effort was shown to vary considerably among members in a smooth-billed ani group by Köster (*6*), but observations were not begun early enough to determine egg-laying order or the loss of eggs by tossing. In three of the groove-billed ani nests in which I could identify the order of laying, the incubation effort of each bird was monitored for 1 to 3 days by direct observation or time-lapse photography. Nestling feeding rates were monitored in one of these nests as well. Relative incubation effort as a function of sex and status is shown in Fig. 1. In all cases, incubation effort increased with increasing status for males but decreased with increasing status for females. The alpha male contributed more than any other bird to daytime incubation and nestling care and, in addition, was the only bird to incubate at night. These results are consistent with those of Köster (*6*), who also noted the inverse relationship of incubation effort between the male and female of a pair and the nighttime incubation effort of that male which incubates most during the day. The same relationship existed for relative nestling feeding rates, but the skew in effort was less and juvenile helpers in the group contributed substantially.

Female behavior in terms of parental effort is reminiscent of parasitism, in which the alpha individual replaces the eggs of low-status individuals with her own and greatly reduces her incubation effort relative to the other females. Males, on the other hand, incubate in direct proportion to their presumed gamete contribution. This latter correlation implies that males "know" the status of their mates. It therefore seems likely that an underlying dominance hierarchy within the group determines laying sequence, mate selection, and incubation effort. The position of an individual in the communal hierarchy thus has important implications for its reproductive success. While it is not the intention of this paper to examine the longer-term effects on lifetime fitness of joining communal groups, the analysis has revealed competition within this cooperative system and may help to explain the losses of eggs in other avian species engaging in communal nesting.

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2. This study was conducted in Guanacaste, Costa Rica, from 1971 to 1973.
3. S. Vehrencamp, thesis, Cornell University (1976).
4. Single pairs with juvenile helpers are an exception, laying significantly more eggs (4.9) than pairs without helpers (Mann-Whitney U test, $n_1 = 14$, $n_2 = 19$, $P < .005$). This effect was not noted for groups with helpers. It suggests that females adjust their clutch size to the total number of birds in the group and not to the number of laying females.
5. For each of 184 nestlings in 25 nests, the percentage of smaller nestmates was calculated. These nestlings were grouped into ten nestmate size categories of 0 to 10 percent, 11 to 20 percent, and so on, and the percentage of nestlings surviving within each category was determined.
6. F. Köster, *Bonn. Zool. Beitr.* **22**, 4 (1971).
7. Supported in part by an NSF Aid-to-Dissertation grant and an NSF traineeship awarded through Cornell University. I thank C. Kagarise for assistance in the field, L. Moore and J. Bradbury for comments on the manuscript, and S. T. Emlen for advice throughout this study.

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